

## GRIT-SITE SELECTION OF BLACK BRANT: PARTICLE SIZE OR CALCIUM CONTENT?

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**ABSTRACT.**—We examined selection of grit-ingestion sites by Black Brant (*Branta bernicla nigricans*) on South Humboldt Bay, California in relation to particle size and calcium content. We hypothesized that Brant site selection was dependent primarily upon calcium content and secondarily upon distribution of substrate particle size. We (1) mapped grit-ingestion sites, (2) ranked their importance by Brant abundance and individual movement probabilities between sites, (3) characterized Brant gizzard grit and compared it with grit available at ingestion sites, and (4) compared calcium content and particle-size distribution between ingestion sites and unused sites, and between primary and secondary ingestion sites. Brant repeatedly congregated at specific, discrete sites during the 2 years of observation. The distribution of gizzard-grit particle size was right-skewed toward larger particles (>0.5 mm) relative to the proportional availability of particle sizes in the substrate. We found no significant differences in calcium content or particle size between sites where grit was ingested and unused sites. Within used sites, the calcium content of substrates at the primary ingestion site was significantly higher than at the secondary ingestion sites, as ranked by Brant abundance and between-site movement probabilities. Our findings from the field corroborate previous laboratory results, and confirm that calcium is a significant ecological factor for this species. Received 14 May 2004, accepted 19 October 2004.

Preferred sites for gizzard-grit ingestion may be used faithfully by wild bird populations for many decades (McIlhenny 1932), but site selection of this resource is understudied. It has long been accepted that gizzard grit (hereafter grit) is an essential aid for grinding food (Leopold 1931), and captive birds deprived of grit experience elevated mortality (McCann 1939). In some waterfowl, amount of grit in the gizzard and size of grit particles are related to diet, with more grit and smaller particles in the gizzards of herbivores compared to omnivores and carnivores (Thomas et al. 1977, Skead and Mitchell 1983). Leopold (1933) proposed that grit could be a source of mineral calcium for birds. This is well-documented only for Ring-necked Pheasant (*Phasianus colchicus*), a species whose grit consumption is driven primarily by the need for calcium and only secondarily as a grinding material (McCann 1939)—and whose distribution and abundance is influenced by the availability of calciferous grit (Leopold 1931; McCann 1939, 1961; Dale

1954). Calcium is a crucial breeding-season nutrient for eggshell and skeleton formation, but historically it has been relatively neglected compared with investigations of fat and protein (Alisauskas and Ankney 1992, but see Ankney 1984). Geese rely to varying degrees upon endogenous reserves for successful breeding (Ankney and MacInnes 1978, Raveling 1979, Prop and Black 1998), and although Black Brant (*Branta bernicla nigricans*) rely on reserves less than other arctic-breeding waterfowl of similar mass (Ankney 1984), Brant skeletal mass (an index of calcium content) is reduced 27% between pre- and post-laying (Ankney 1984). Trost (1981) reported that grit consumption by captive female Mallards (*Anas platyrhynchos*) peaks in the spring pre-breeding period; Mallards demonstrate selectivity in both particle size and calcium content. Additionally, a calcium-deficient diet reduces the breeding success of Great Tits (*Parus major*; Graveland and Drent 1997), implying that calcium may be important to breeding birds across taxa.

Here, we examine selection of grit-ingestion sites by Black Brant on South Humboldt Bay, California. Our objective was to examine how calcium and particle size affect site use by Brant, hypothesizing that selection of grit-ingestion sites was dependent primarily upon calcium content and secondarily upon the frequency distribution of particle size. We (1)

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mapped Brant grit-ingestion sites; (2) ranked site importance by Brant abundance and individual movement probabilities between sites; (3) characterized gizzard grit from two time periods, and compared it with grit available at ingestion sites; and (4) compared calcium content and frequency distribution of particle size between ingestion sites and unused sites, and between primary and secondary ingestion sites.

## METHODS

*Study species and site.*—The Black Brant is a small sea goose that breeds and molts in western and northern Alaska, Russia, and the Northwest Territories (Reed et al. 1998). In fall, most Black Brant stage at Izembek Lagoon, Alaska, before migrating south, non-stop, to coastal lagoons of Washington, Oregon, California, Baja California, and Mexico (Reed et al. 1998). During winter and spring, Brant head north again toward breeding grounds in the western Nearctic (Reed et al. 1998). Northward migration is composed of shorter, stepping-stone flights between stopovers at bays and estuaries along the west coast of North America (Reed et al. 1998). We conducted our study at South Humboldt Bay, California (Fig. 1), an important stopover site for Black Brant during their northward migration to the breeding grounds (Moore et al. 2004). Brant begin arriving at Humboldt Bay in mid-December, peak at ~14,000 birds in mid-March, and before April the majority have departed Humboldt Bay (U.S. Fish and Wildlife Service unpubl. data).

Humboldt Bay is a 62-km<sup>2</sup> estuary (Barnhart et al. 1992); 1,044 ha of eelgrass (*Zostera marina*) occurs in discrete beds interlaced with a dendritic network of channels. Black Brant feed almost exclusively on eelgrass during the non-breeding season, and because Brant do not dive, eelgrass can only be accessed at low tides (Derksen and Ward 1993). South Humboldt Bay contains 70% of the eelgrass beds found in Humboldt Bay, and supports 78–94% of the Brant that use Humboldt Bay each year (Moore et al. 2004). From 350 km to the south to 600 km to the north, Humboldt Bay is the only large estuary containing substantial beds of eelgrass (>300 ha)—effectively making it an insular study area with low

potential for regional movements (Moore et al. 2004).

South Spit, the sandy peninsula separating South Humboldt Bay from the Pacific Ocean, has one large and many small intertidal sandbars along its eastern shoreline that are used by Brant to rest, preen, and ingest grit as the tide ebbs (Fig. 1). These sandbars are exposed early in the ebb, long before the water level is low enough to allow Brant access to the eelgrass beds. As soon as the substrate is within ~0.3 m of the water surface, Brant flock to the sandbar sites to ingest grit.

*Observations.*—We conducted 88 Brant surveys of South Bay to identify and map the principle grit-ingestion sites. In 2000, we surveyed the bayside beach of South Spit from a vehicle on South Spit Road (which runs along the bay shore) 24 times during daylight ebbing tides January–April; the abundance and distribution of all Brant were mapped on an aerial photo of South Humboldt Bay, and grit-ingestion behavior was noted. To better observe all of South Bay in 2001, in addition to 31 South Spit Road surveys, we surveyed the entire South Bay 33 times during daylight ebbing tides in February and March using a 60× spotting scope from an elevated observation site (Bell Hill in Fig. 1); the abundance and distribution of all Brant were mapped on an aerial photo of South Humboldt Bay, and grit-ingestion behavior was noted. We identified 10 main haul-out sites, and observed grit-ingestion behavior at 6 of these (Fig. 1). We based our analyses of grit selection on the three most used grit-ingestion sites (A, B, and C in Fig. 1) used by 78% of all Brant.

*Movement.*—To estimate movement probabilities between grit-ingestion sites, we read tarsal bands of all Brant at the three most used grit-ingestion sites (A, B, and C in Fig. 1). Brant were banded at major breeding and molting locations; all ages of individual Black Brant have been marked annually with uniquely coded tarsal bands resulting in ~8% of the total population being banded (Sedinger et al. 1993, Ward et al. 1993, Bollinger and Derksen 1996). On 24 days between January and April 2000, we used a 60× spotting scope on the bay-side shore of South Spit to read the leg bands of Brant ingesting grit at South Spit sandbars during ebbing tides.

We used multi-strata modeling in program

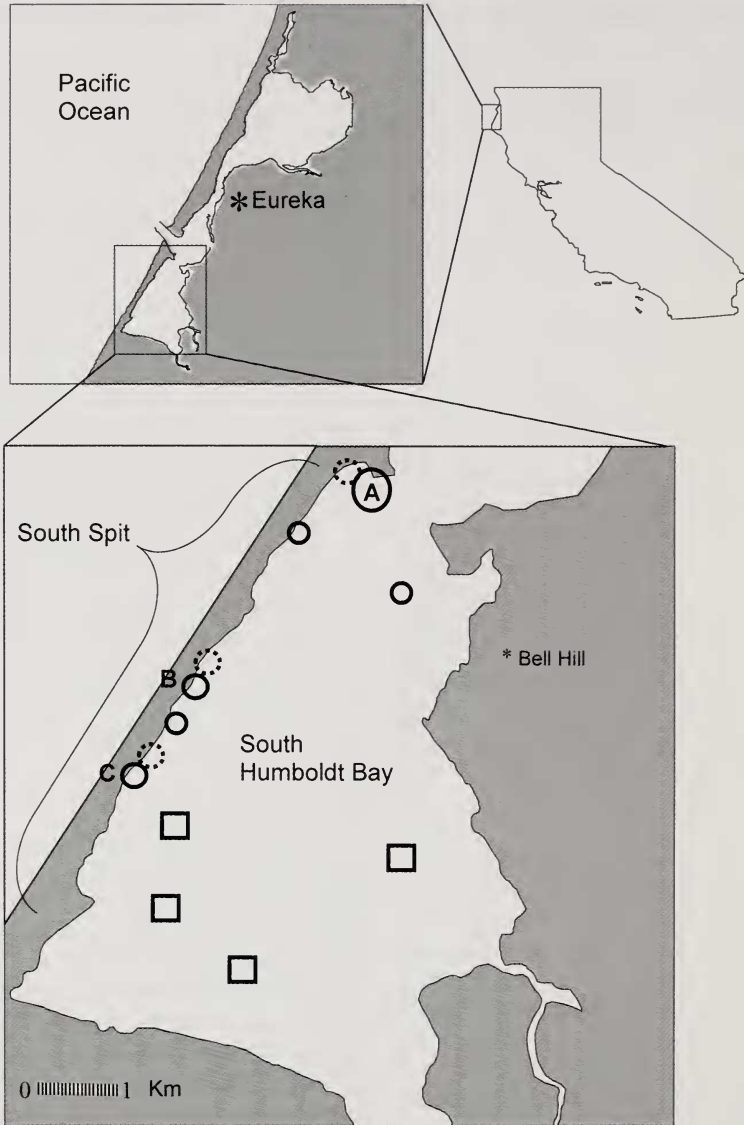


FIG. 1. Study area on South Humboldt Bay, California. Black Brant (*Branta bernicla nigricans*) using grit-ingestion sites were observed from Bell Hill. Grit-ingestion sites are marked with solid-line circles (main sites are labeled A, B, and C). Paired, unused, substrate-sampling sites are indicated by broken-line circles. Roost sites with very fine sediments that were not sampled are indicated with squares.

MARK (White and Burnham 1999) to estimate probabilities of banded Brant moving between grit-ingestion sites. Two strata were defined: North (site A), and South (sites B and C). Sites B and C were combined based on their proximity and to make the number of individuals in each strata more equivalent. Model selection was based in Akaike's information criterion corrected for small sample

size ( $AIC_c$ ) (Akaike 1974, Burnham and Anderson 1998). All models were run using the logit link function. Goodness-of-fit (GOF) was assessed in a recaptures-only data structure using the bootstrap procedure in program MARK with 100 simulations. The general model for GOF testing was  $\{S(\text{site} \times \text{time}) p(\text{site} \times \text{time})\}$ , indicating that local study area fidelity ( $S$ ) and recapture ( $p$ ) probabilities



varied by site and time. We accepted a general model GOF if its deviance ranked <90 out of the 100 rank-ordered deviances simulated.

Due to weather and tides, leg bands could not be read every day to estimate daily movement probabilities; therefore, we pooled the 24 days of band-reading observations into twelve 7-day intervals. Different pooling intervals were tried with the final selection being the shortest time period that met three criteria: (a) the number of observation periods with no data was 0, (b) the rank of the deviance of the general model was <90th out of 100 ranked bootstrap simulations, and (c) the general multi-strata model  $\{S(\text{site} \times \text{time}) p(\text{site} \times \text{time}) \psi(\text{site} \times \text{time})\}$  would converge. Temporal pooling violates the assumptions of instantaneous observations and of a closed population during observations, and can lead to biased parameter estimates (Hargrove and Borland 1994); however, pooling was necessary to estimate movement rates and is commonly practiced (Pradel et al. 1997, Reed et al. 1998).

The *a priori* model set included  $S$ ,  $p$ , and  $\psi$  (movement probability) as constants ( $\cdot$ ), time-dependent (time), and linear trends through time (T), with site effects modeled as (site), (site + time), (site + T), (site  $\times$  time), and (site  $\times$  T), for a total of eight models for each parameter. We simplified the general model systematically, starting with  $p$ , then reducing  $S$  and  $\psi$  in turn for a total of 24 models tested altogether (Lebreton et al. 1992). The general model  $\{S(\text{site} \times \text{time}) p(\text{site} \times \text{time}) \psi(\text{site} \times \text{time})\}$  was reduced by first ranking all eight models for  $p$  in the set while holding  $S$  and  $\psi$  in their general form. After a parsimonious model of  $p$  was found,  $S$  was reduced by ranking all eight models for  $S$  in the set while holding  $p$  in its most parsimonious form, and  $\psi$  in its general form. Finally,  $\psi$  was reduced by ranking all eight models for  $\psi$  in the set while holding  $p$  and  $S$  in their most parsimonious form (Lebreton et al. 1992). The model with the lowest  $AIC_c$  value was considered the best or most parsimonious model. Akaike weights (Burnham and Anderson 1998) were computed to denote relative strength of evidence supporting each model.

Often, several models in the final set of top-ranked models appear equally plausible, with  $\Delta AIC_c$  values near zero and  $AIC_c$  weights

comparable to the best model. To account for model selection uncertainty, model averaging was used to create parameter estimates (Burnham and Anderson 1998). Model averaging uses  $AIC_c$  weights to calculate the weighted average of each real parameter across all models with  $AIC_c$  weights greater than zero.

*Grit sampling.*—To compare gizzard grit with grit available at grit-ingestion sites, we obtained hunter-donated gizzards to characterize particle-size distributions of gizzard grit. We sampled substrates at grit-ingestion sites and compared those to gizzard grit to determine whether differential selection of particles was occurring. To determine whether calcium content or particle size distribution was the main site-selection factor, we also compared substrate samples from used and unused sites, and between used sites.

During November 2000 and January 2001, hunters donated gizzards, wings, and heads from Brant taken on Humboldt Bay. November gizzards were more likely to be from birds newly arrived from Izembek Lagoon, Alaska, whereas January gizzards were more likely to be from birds either newly arrived from a more southerly stopover site, or from birds overwintering on Humboldt Bay. Extraneous portions of the alimentary canal and fat deposits were removed, gizzards were opened, and all contents washed into a container. Empty gizzard wet weight (g), head length (mm), age (adult or juvenile based on plumage characteristics), and month taken (November or January) were recorded for each bird. Color of the gizzard grit was classified as either predominantly white or black in order to assign its geographic origin. Organic matter was removed from gizzard-grit samples by ignition at 500°C for 4 hr. After removal of organic matter, grit samples were dried at 105°C for 24 hr and filtered through a stack of five sieves (mesh sizes: 0.053, 0.106, 0.25, 0.5, 1.0, and 2.0 mm) for 5 min in a sediment shaker; portions then were weighed. Proportions (by weight) were arcsine transformed for analysis (Zar 1974).

During low tides of 1 and 15 April 2001, we sampled substrate at the three grit-ingestion sites on South Spit with highest mean Brant abundance, and at paired, unused sites within 50 m of used sites. Five samples were collected at each site except at used site A,

TABLE 1. Table of model selection results for local fidelity ( $S$ ), recapture ( $p$ ), and movement ( $\psi$ ) probabilities of 322 Black Brant (*Branta bernicla nigricans*) ingesting grit at two sites on South Humboldt Bay, California, 2000. While the best model (boldface,  $\Delta AIC_c = 0$ ) indicated no difference in movement probability between sites, the two next-best models did include site, and had non-trivial  $AIC_c$  weights, thus contributing a substantial site effect (a north-biased movement probability) to the final model-averaged parameter estimates.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weights	$k$	Deviance
<b>{<math>S(T)</math> <math>p(\text{site} + \text{time})</math> <math>\psi(\cdot)</math>}<sup>a</sup></b>	687.4	0	0.37	15	241.7
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site})$ }	687.7	0.3	0.31	16	239.9
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site} \times T)$ }	689.1	1.7	0.16	18	236.9
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(T)$ }	689.6	2.2	0.12	16	241.7
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site} + T)$ }	691.7	4.3	0.04	17	241.6
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site} + \text{time})$ }	697.9	10.5	0	26	227.5

<sup>a</sup> T = linear temporal trend, site = difference between north and south sites, time = full time dependence, (·) = constant.

where we collected seven samples. Each sample was a volume equivalent to approximately 30 g (dry weight) of sand collected from within 1.5 cm of the surface. Samples were taken at 5-m intervals along a transect that began 10 m down slope from the high tide line, and ran along the ridge of each sandbar toward the water line. In spring 2001, at Izembek Lagoon, Alaska, we also obtained two substrate samples (~30 g each) from the intertidal zone of one of the most heavily used grit-ingestion sites. All substrate samples were dried, filtered, and weighed using the same method described above for analyzing samples of gizzard grit. Our analyses relied upon the assumption that the gizzard grit we collected was ingested from the sites we sampled at Izembek Lagoon and Humboldt Bay. There is no way to confirm the validity of this assumption, but based on the appearance and mineral composition of the grit particles, we are confident they came from the bays in question, if not necessarily from the sampled sites.

To determine calcium content of substrate samples, we used a sample splitter to split entire ~30-g substrate samples, one portion of which was split again to obtain ~7-g samples. Samples were dried at 105° C for 24 hr, cooled in a desiccator, and weighed. Calcium carbonate content was estimated by measuring the volume of gas evolved (corrected for sample weight, temperature, and pressure conditions) when 10 ml of 6 N hydrochloric acid was added to the sample and stirred for 5 min (detailed methods in Machette 1986, modified from Dreimanis 1962). Percent calcium carbonate of each sample was arcsine trans-

formed for analysis (Zar 1974). We used GLM in program NCSS (Hintze 2000) to analyze all gizzard grit and substrate data. Means are reported  $\pm$  SE.

## RESULTS

Based on 88 surveys, Brant repeatedly hauled out at 10 specific sandbars along South Spit and at fine-sediment bars within the bay (Fig. 1). These sites were discrete and their use by Brant did not change between the 2 years of observation, nor within an observation season. Sites A, B, and C combined were used by 78% of all Brant. Site A, the northernmost grit-ingestion site (Fig. 1), was used by more Brant (site A: mean = 342 birds  $\pm$  73, maximum = 1,580) than the two sites with next-highest abundance estimates (site B: mean = 94  $\pm$  25, maximum = 250; site C: mean = 105  $\pm$  53, maximum = 200). Fine-sediment bars around the perimeters of eelgrass beds were also used by Brant hauling out during ebb tides, but grit ingestion at these sites was not documented.

Based on 322 individual encounter histories, the most parsimonious model of  $\psi$  (the probability of an individual moving between strata each week) between North (site A) and South (sites B and C) was constant (Table 1), but model-averaged parameters indicated North-biased  $\psi$  (North to South:  $\psi = 0.123 \pm 0.054$ ; South to North:  $\psi = 0.287 \pm 0.124$ ). The most parsimonious model of  $S$  indicated no difference in local study area fidelity between sites (Table 1). Based on the number of Brant using grit-ingestion sites, and movement probabilities between the sites, we designated the northern site (A) as the primary

TABLE 2. Weight (SE) of gizzards and grit found in the gizzards of Black Brant (*Branta bernicla nigricans*) shot at Humboldt Bay, California, in November 2000 and January 2001.

	November 2000 (n = 31)	January 2001 (n = 14)	P-value <sup>a</sup>
Gizzard wet weight (g)	72.5 (9.9)	102.8 (5.9)	<0.001
Grit-sand weight (g)	6.9 (0.3)	10.0 (0.5)	0.001
Gizzard weight/sand weight	10.5	10.3	
Grit color	Black	White	

<sup>a</sup> From *t*-test statistic.

grit-ingestion site, and southern sites (B and C) as secondary grit-ingestion sites.

The activities of Brant observed at the South Spit sandbars were tide-dependent. When water depth over the sandbars was >0.5 m, no Brant were present. When water depth was <0.5 m, but sandbars were still submerged, rafts of up to hundreds of birds would jostle over the still-submerged sandbars, rapidly upending then coming up with mouths overflowing with sand solution. Once the sandbars became exposed as tide waters receded, the few birds still ingesting grit were found at the perimeters of the sandbars or at puddles of water remaining on sandbar surfaces. The three main grit-ingestion sites we focused on were exposed by ebbing tides at nearly the same water level (1.8–1.6 m above MLLW), so no tidally induced sequence of accessibility was present.

Hunters donated 31 gizzards in November and 14 in January. All gizzards collected in November were significantly shrunken due to the birds having recently undertaken their non-stop southward migration. November gizzards contained significantly less grit than those collected from Brant during their "stepping-stone" northward migration in January, although the ratio of gizzard weight to grit weight remained constant between seasons (Table 2). After controlling for month of collection, neither gizzard weight, nor grit-sand weight differed significantly between adult and juvenile birds; thus, ages were pooled for subsequent analyses. Grit samples from birds collected in November contained predominantly black volcanic sand, indicating an origin at Izembek Lagoon, Alaska, the primary fall staging area for Brant (D. H. Ward pers. comm.). Grit samples from birds collected in January contained predominantly white quartz sand—as found at known Brant stopover sites

from Baja California north to Humboldt Bay (DEL pers. obs., D. H. Ward pers. comm.).

We compared particle-size distributions of gizzard grit collected in November with substrate from grit-ingestion sites at Izembek Lagoon (Fig. 2A), and we compared gizzard grit collected in January with substrate collected from grit-ingestion sites at Humboldt Bay (Fig. 2B). In November, gizzard grit was composed mostly of 0.5–1.0 mm particles. In January, gizzard grit was made up of nearly equal proportions of particles 0.25–0.5 and 0.5–1.0 mm in size. Substrate at both Izembek Lagoon and Humboldt Bay was composed of mostly particles 0.25–0.5 mm in size. In both seasons, distributions of gizzard-grit particle size were right-skewed toward larger particles (>0.5 mm) relative to the proportional availability of particle sizes in the substrate (Fig. 2A, B).

We compared particle-size distributions of substrate sand from ingestion sites with sand from unused sites in Humboldt Bay (Fig. 3). We found no differences in particle size distributions between sites where grit was ingested and unused sites. We also compared particle size distributions of sand from primary (site A, north site) and secondary (sites B and C, south sites) ingestion sites (Fig. 4). Relative to the north site, the south sites' distribution was right-skewed, containing larger proportions of particles 0.25–0.5 and 0.5–1.0 mm in size (Fig. 4).

The mean calcium content (proportion calcium carbonate) of substrate from all grit-ingestion sites used by Brant (mean = 0.100 ± 0.042) was not significantly higher ( $t = -0.88$ ,  $df = 31$ ,  $P = 0.19$ ) than at unused sites (mean = 0.088 ± 0.034). However, the calcium content of substrates at the primary ingestion site (site A: mean = 0.137 ± 0.036) was significantly higher ( $t = -5.01$ ,  $df = 15$ ,  $P < 0.001$ ) than at the secondary ingestion



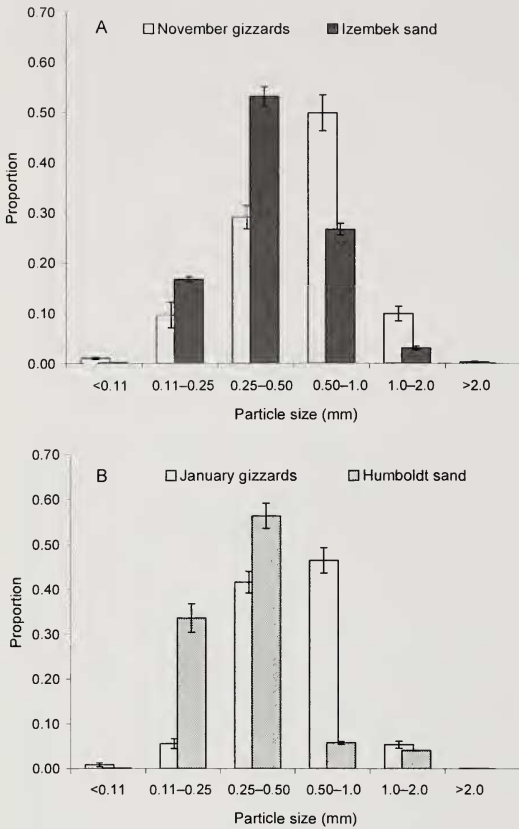


FIG. 2. Particle-size distributions (mean  $\pm$  SE) of gizzard grit from Black Brant (*Branta bernicla nigricans*) collected at Humboldt Bay, California in November 2000 compared with substrate from grit-ingestion sites at Izembek Lagoon, Alaska (A); and gizzard grit collected at Humboldt Bay, California in January 2001 compared with substrate from grit-ingestion sites at Humboldt Bay (B).

sites (sites B and C combined: mean = 0.073  $\pm$  0.018).

DISCUSSION

We documented repeated use by Brant, within and between seasons, of discrete grit-ingestion sites on South Humboldt Bay. Used sites were characterized by differential abundance and constant, low levels of asymmetrical movement by individual Brant between sites. These differences were used to rank the sites as primary and secondary in importance. Only at the level of “within used sites” was there any evidence of differential selection. Our results within used sites indicate that Brant select grit-ingestion sites primarily

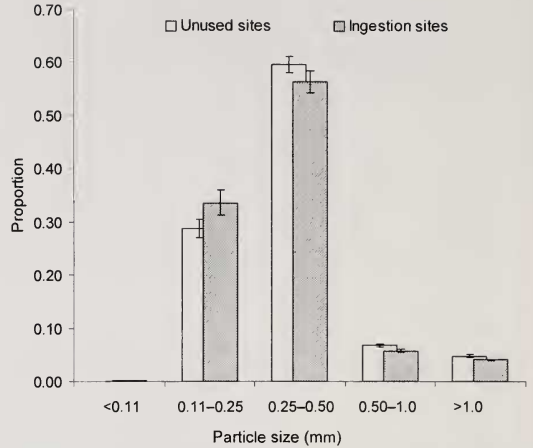


FIG. 3. Particle-size distributions (mean  $\pm$  SE) for substrate sand at grit-ingestion sites versus sites not used by Black Brant (*Branta bernicla nigricans*) on South Spit, South Humboldt Bay, California, 2000–2001.

based upon calcium carbonate content of the substrate, and secondarily based upon availability of particle size. These results from field data corroborate the laboratory-based findings of McCann (1939) for Ring-necked Pheasants and Trost (1981) for Mallards.

We interpreted movement toward the preferred site as being calcium driven. That the most preferred grit-ingestion site had higher amounts of calcium carbonate is not surprising considering that eggs are composed of 10–

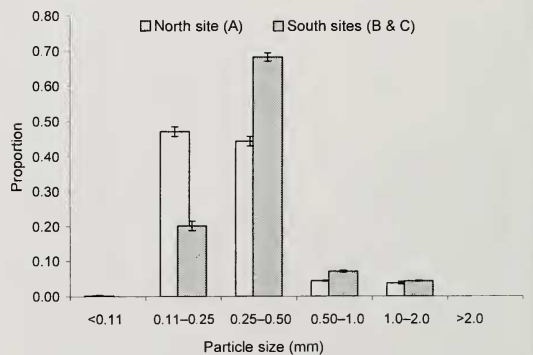


FIG. 4. Particle-size distributions (mean  $\pm$  SE) for substrate sand at primary (A) and secondary (B & C) grit-ingestion sites used by Black Brant (*Branta bernicla nigricans*) on South Spit, South Humboldt Bay, California, 2000–2001. Sites were ranked as primary or secondary according to bird abundance and between-site movement probabilities.

15% calcium (Gilbert 1971) and Brant eggshells average  $8.2 \pm 0.1$  g calcium (Ankney 1984). Calcium deficiency has been linked with reduced reproductive success in Great Tits (Graveland and Drent 1997). Graveland and Van Gijzen (1994) found that Great Tits could not obtain sufficient calcium from arthropod and seed food items, but required calcium-rich supplementary material to meet the demands of egg laying. Although Brant are less reliant on endogenous reserves of fat and protein than other arctic-breeding waterfowl due to rich food sources being available near the nest (Ankney 1984), all the calcium requirements of the eggs must be available at the time of laying. For egg formation, birds mobilize calcium from the skeleton and medullary bone (Taylor and Moore 1954, Simkiss 1967), calcium that must be obtained and stored during the nonbreeding season.

Movement toward secondary grit-ingestion sites could have been due to calcium satiation, slightly greater levels of the preferred (larger) grit-particle sizes at secondary sites, displacement by more dominant competitors, and/or avoidance of disturbance. The difference in proportions of particles 0.5–1.0 mm in size between the primary and secondary sites was small, but the difference in handling times required to filter out sufficient quantities of these particles during opportune tidal windows may be enough to explain the attraction to secondary sites where the preferred particle sizes are more abundant. Levels of agonistic behavior were not documented in our study to establish whether competition might drive the movement toward the secondary sites. Brant, however, are sensitive to anthropogenic disturbances (Schmidt 1999), and disturbance may have influenced some of their movements to secondary sites. The primary site is near the main ship channel between South Humboldt Bay docks and both North Humboldt Bay and the Pacific Ocean, while the secondary sites are more remote from human activities.

We found no difference between used and unused sites with respect to particle size or calcium content. No other factors were investigated, thus the factor responsible for specific site use by Black Brant at Humboldt Bay remains unclear. It could have been a function of scale in our experimental design (i.e., se-

lecting paired unused sites at a scale that biased the results toward no difference). A random selection of the comparison sites might have revealed differences. Selection of grit-ingestion sites likely represents a complex interaction of nutritional requirements, social factors, and grit availability.

The right-skewed particle-size distributions of grit found in Brant gizzards versus samples of substrate sand could indicate the ability of Brant to ingest larger sand particles; alternatively, it may reflect differential retention times in the gizzard for different particle sizes. We believe the difference is due to selective ingestion because the only study of gizzard particle retention in waterfowl (using captive Mallards) found no difference in retention rates for particles of different size classes (Trost 1981). Wear (reduction of grit size while resident in the gizzard) could induce only a left-skewed distribution relative to available particle sizes. There is some disagreement over the mechanism waterfowl use to selectively ingest grit particles (Crome 1985, Kooloos et al. 1989, Nudds 1992, Nudds and Wickett 1994, Mateo et al. 2000), but whatever process the birds use, grit-ingestion behavior was much more prevalent when sandbars were still submerged, indicating that Brant prefer to ingest grit when it is in suspension.

Calcium as an essential resource should be more closely examined in grit and food supplies at stopover and breeding sites for all species of migratory birds. Similar studies of newly hatched precocial birds, which need calcium most for skeletal development, would also be instructive. Additionally, calcium requirements for successful reproduction and the ability of various species to store and mobilize skeletal calcium should be determined precisely.

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### LITERATURE CITED

- AKAIKE, H. 1974. A new look at statistical model identification. *IEEE Transactions on Automatic Control* AC19:716–723.
- ALISAUSKAS, R. T. AND C. D. ANKNEY. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30–61 in *Ecology and management of breeding waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- ANKNEY, C. D. 1984. Nutrient reserve dynamics of breeding and molting Brant. *Auk* 101:361–370.
- ANKNEY, C. D. AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459–471.
- BARNHART, R. A., M. J. BOYD, AND J. E. PEQUEGNAT. 1992. The ecology of Humboldt Bay California: an estuarine profile. Biological Report, no. 1. U.S. Fish and Wildlife Service, Washington, D.C.
- BOLLINGER, K. S. AND D. V. DERKSEN. 1996. Demographic characteristics of molting Black Brant near Teshekpuk Lake, Alaska. *Journal of Field Ornithology* 67:141–158.
- BURNHAM, K. P. AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- CROME, F. H. J. 1985. An experimental investigation of filter feeding on zooplankton by some specialized waterfowl. *Australian Journal of Zoology* 33: 849–862.
- DALE, F. H. 1954. Influence of calcium on the distribution of the pheasant in North America. *Transactions of the North American Wildlife Conference* 19:316–323.
- DERKSEN, D. V. AND D. H. WARD. 1993. Life history and habitat needs of the Black Brant. *Fish and Wildlife Leaflet* 13.1.15. U.S. Fish and Wildlife Service, Washington, D.C.
- DREIMANIS, A. 1962. Quantitative gasometric determination of calcite and dolomite by using Chittick apparatus. *Journal of Sedimentary Petrology* 32: 520–529.
- GILBERT, A. B. 1971. The egg: its physical and chemical aspects. Pages 1379–1399 in *The physiology and biochemistry of the domestic fowl* (D. J. Bell and B. M. Freeman, Eds.). Academic Press, New York.
- GRAVELAND, J. AND R. H. DRENT. 1997. Calcium availability limits breeding success of passerines on poor soil. *Journal of Animal Ecology* 66:279–288.
- GRAVELAND, J. AND T. VAN GIJZEN. 1994. Arthropods and seeds are not sufficient as calcium sources for shell formation and skeletal growth in passerines. *Ardea* 82:299–314.
- HARGROVE, J. W. AND C. H. BORLAND. 1994. Pooled population parameter estimates from mark-recapture data. *Biometrics* 50:1129–1141.
- HINTZE, J. L. 2000. Number cruncher statistical system: NCSS 2000. Kaysville, Utah.
- KOOLOS, J. G. M., A. R. KRAAIJEVELD, G. E. J. LANGENBACH, AND G. A. ZWEERS. 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata*, and *Aythya fuligula* (Aves, Anseriformes). *Zoomorphology* 108:269–290.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LEOPOLD, A. 1931. Report on a game survey of the north central states. Democrat Printing Company, Madison, Wisconsin.
- LEOPOLD, A. 1933. Game management. Charles Scribner's Sons, New York.
- MACHETTE, M. N. 1986. Calcium and magnesium carbonates. Pages 30–33 in *Field and laboratory procedures used in a soil chronosequence study* (M. J. Singer and P. Janitzky, Eds.). U.S. Geological Survey Bulletin, no. 1648.
- MATEO, R., R. GUITART, AND A. J. GREEN. 2000. Determinants of lead shot, rice, and grit ingestion in ducks and coots. *Journal of Wildlife Management* 64:939–947.
- MCCANN, L. J. 1939. A study of the grit requirements of certain gallinaceous game birds. *Journal of Wildlife Management* 3:31–41.
- MCCANN, L. J. 1961. Grit as an ecological factor. *American Midland Naturalist* 65:187–192.
- MCILHENNY, E. A. 1932. The Blue Goose in its winter home. *Auk* 49:279–306.
- MOORE, J. E., M. A. COLWELL, R. L. MATHIS, AND J. M. BLACK. 2004. Staging of Pacific flyway Brant in relation to eelgrass abundance and site isolation, with special consideration of Humboldt Bay, California. *Biological Conservation* 115:475–486.
- NUDDS, T. D. 1992. Patterns in breeding waterfowl communities. Pages 540–567 in *Ecology and management of breeding waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- NUDDS, T. D. AND R. G. WICKETT. 1994. Body size and seasonal coexistence of North American dabbling ducks. *Canadian Journal of Zoology* 72:779–782.
- PRADEL, R., N. RIOUX, A. TAMISIER, AND J.-D. LEBRETON. 1997. Individual turnover among wintering teal in Camargue: a mark-recapture study. *Journal of Wildlife Management* 61:816–821.
- PROP, J. AND J. M. BLACK. 1998. Food intake, body reserves and reproductive success of Barnacle Geese *Branta leucopsis* staging in different habitats. *Norsk Polarinstittutt Skrifter* 200:175–193.
- RAVELING, D. G. 1979. The annual cycle of body composition in Canada Geese with special reference to the control of reproduction. *Auk* 96:234–252.
- REED, E. T., E. G. COOCH, F. COOKE, AND R. A. GOUDIE. 1998. Migration patterns of Black Brant in

- Boundary Bay, British Columbia. *Journal of Wildlife Management* 62:1522-1532.
- SCHMIDT, P. E. 1999. Population counts, time budgets, and disturbance factors of Black Brant (*Branta bernicla nigricans*) at Humboldt Bay, California. M.Sc. thesis, Humboldt State University, Arcata, California.
- SEDINGER, J. S., C. J. LENSINK, D. H. WARD, R. M. ANTHONY, M. L. WEGE, AND G. V. BYRD. 1993. Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. *Wildfowl* 44:49-59.
- SIMKISS, K. 1967. Calcium in reproduction and physiology. Chapman and Hall, London, United Kingdom.
- SKEAD, D. M. AND R. J. H. MITCHELL. 1983. Grit ingested by waterfowl in relation to diet. *South African Journal of Wildlife Research* 13:32-34.
- TAYLOR, T. G. AND J. H. MOORE. 1954. Skeletal depletion in hens laying on a low calcium diet. *British Journal of Nutrition* 8:112-124.
- THOMAS, G. J., M. OWEN, AND P. RICHARDS. 1977. Grit in waterfowl at the Ouse Washes, England. *Wildfowl* 28:136-138.
- TROST, R. E. 1981. Dynamics of grit selection and retention in captive Mallards. *Journal of Wildlife Management* 45:64-73.
- WARD, D. H., D. V. DERKSEN, S. P. KHARITONOV, AND V. V. BARANYUK. 1993. Status of Pacific Black Brant *Branta bernicla nigricans* on Wrangel Island, Russian Federation. *Wildfowl* 44:39-48.
- WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120-S139.
- ZAR, J. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.